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Re-examination of growth estimates in oceanic squids: the case of *Kondakovia longimana* (Onychoteuthidae)[1]

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Earlier work by the second author on the growth of oceanic squids, based on size-frequency distributions of beaks sampled from sperm whale stomachs and on structural marks on those beaks, showed that these squids apparently had growth rates far in excess of those reported for the fastest-growing fishes, e.g. bluefin tuna. The application of recently developed methods for analysis of length-frequency distributions to some of these earlier data, and new approaches for assessing and comparing the growth performance of fish and aquatic invertebrates, suggest the need for a downward revision of these high growth estimates. This is illustrated here with data on *Kondakovia longimana* (Cephalopoda, Onychoteuthidae) sampled off Durban and Donkergat, South Africa, in the early to mid-1960s.

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Introduction

It has been often stated by marine biologists working on squids that their various adaptations make them very fast-growing animals, more so than fishes (O'Dor *et al.*, 1980; Erhardt *et al.*, 1983; Lee *et al.*, 1989). In this paper earlier estimates of growth in *Kondakovia longimana* (Onychoteuthidae) are reassessed, using recently developed methods for the estimation of growth from size-frequency data and for the comparison of growth performance across taxa. This reassessment is intended to

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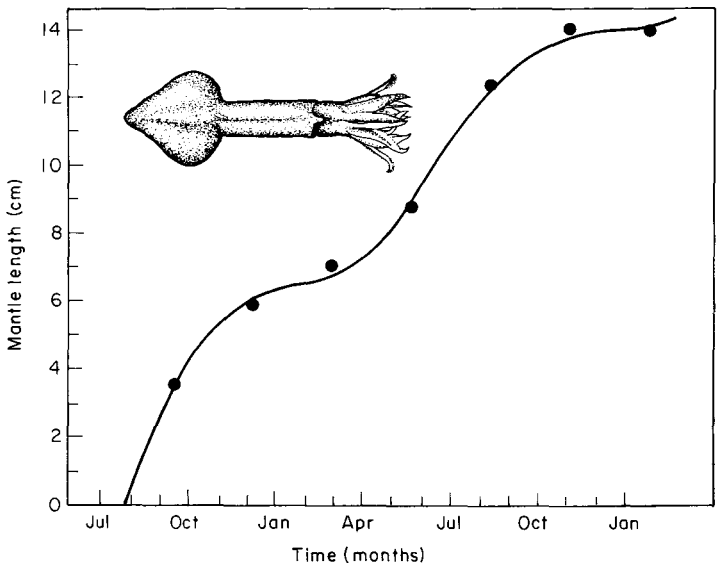

Figure 1. Seasonally oscillating growth curve for *Loligo opalescens* sampled at the Monterey Market, California, as obtained by fitting Equation (1) to size-at-age data of Spratt (1978, Fig. 1). $ML_\infty = 20.8$ cm, $K = 0.755\ yr^{-1}$, $C = 0.85$, $WP = 0.08$ year. (see Table 3 for data sources).

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Table 1. Frequency distribution of lower beak length (ML = class midpoints, in cm) of *Kondakovia longimana* collected from sperm whale stomachs in Durban (1962–1964) and Donkergat (1962–1963). (Data from Clarke, 1980, grouped by months, irrespective of year.)

ML/month	May	Jun	Jul	Aug	Sep
Durban					
0.85		2			
0.95		1			
1.05	1	12	1	1	1
1.15	2	15	10	11	10
1.25	6	41	13	22	18
1.35	14	46	32	32	25
1.45	25	53	34	15	7
1.55	24	74	24	13	4
1.65	52	106	14	7	2
1.75	47	90	6	10	2
1.85	23	39	2	10	1
1.95	10	7	1	4	
Sum	204	486	137	125	70

ML/month	Apr	May	Jun	Jul	Sep	Oct
Donkergat						
1.05	1	3		2		
1.15	1	0		3		
1.25	4	9	2	11	3	8
1.35	8	24	7	25	1	5
1.45	20	39	10	46	2	10
1.55	13	74	11	30	3	6
1.65	10	75	33	21	1	5
1.75	6	64	27	9	0	4
1.85	3	34	10	4	1	2
Sum	66	322	100	151	11	40

Table 2. Relationship between number of apparent growth bands on beaks of *Kondakovia longimana* and the mean wall lengths of these beaks (from Clarke, 1980).

Band no.	Mean wall length of beaks at end of growth period (cm)	No. of beaks in sample
1	0.49	150
2	0.83	150
3	1.13	148
4	1.34	131
5	1.51	112
6	1.67	93
7	1.81	83
8	1.92	60
9	2.02	41
10	2.08	22
11	2.23	11
12	2.06	6

establish not only a range of "possible" growth parameters for *K. longimana*, but also for other – as yet unstudied – squid species. Further, we shall suggest that squids do not grow faster than fishes of the family Scombridae (i.e. the mackerels and tunas), which have the fastest growth among fishes.

This contribution builds on an earlier paper (Pauly, 1985) in which evidence was presented showing that the growth of squids, like that of fishes, oscillates seasonally and that the growth models used to fit size-at-age data of squids should take this explicitly into account (see also Fig. 1).

Material and methods

Estimation of growth parameters

The seasonally oscillating growth model used here was developed independently by Hoenig and Choudary Hanumara (1982) and Somers (1988) and has the form:

$$L_t = L_\infty *(1 - \exp(- K*(t - t_0) - S_1 + S_2)) \quad (1)$$

where

$$S_1 = C*K/(2*\pi)*\sin(t - t_0)$$
$$S_2 = C*K/(2*\pi)*\sin(t_0 - t_s)$$

and L_t = length at time t, L_∞ = asymptotic length, K = growth parameter of dimension time^{-1}, t = time (age; in year), t_0 = "age" at length 0, t_s = starting-point of oscillations with respect to $t_0 = 0$, C = parameter expressing the amplitude of the oscillations. (Note that for fitting purposes, t_s is replaced by a "Winter Point", i.e. the period of the year when growth is lowest; $WP = t_s + 0.5$).

This seasonally oscillating growth curve is constructed such that the growth parameter K is directly comparable to the growth parameter of the non-seasonal von Bertalanffy growth equation (a non-seasonal growth equation, fitted (but necessarily less well) to the data in Figure 1 by means of a von Bertalanffy plot, yielded an estimate of $K = 0.79\ yr^{-1}$).

Equation (1) was fitted to size-frequency distributions of lower beaks of *K. longimana* from Clarke (1980), derived from sperm whale stomachs sampled at Durban and Donkergat, South Africa, in 1962–1964 and 1962–1963, respectively (Table 1). The fitting was carried out using a non-parametric method, the ELEFAN I program of Pauly and David (1981), as implemented by Gayanilo *et al.* (1988).

However, because of the variability of the data in question (see below), the size frequencies in Table 1 could not be used to estimate all parameters of Equation (1). Instead, plausible values of the parameters L_∞, C, and WP were postulated, and the goodness-of-fit index of the ELEFAN I program (Rn, roughly analogous to the coefficient of determination or r^2 of parametric methods)

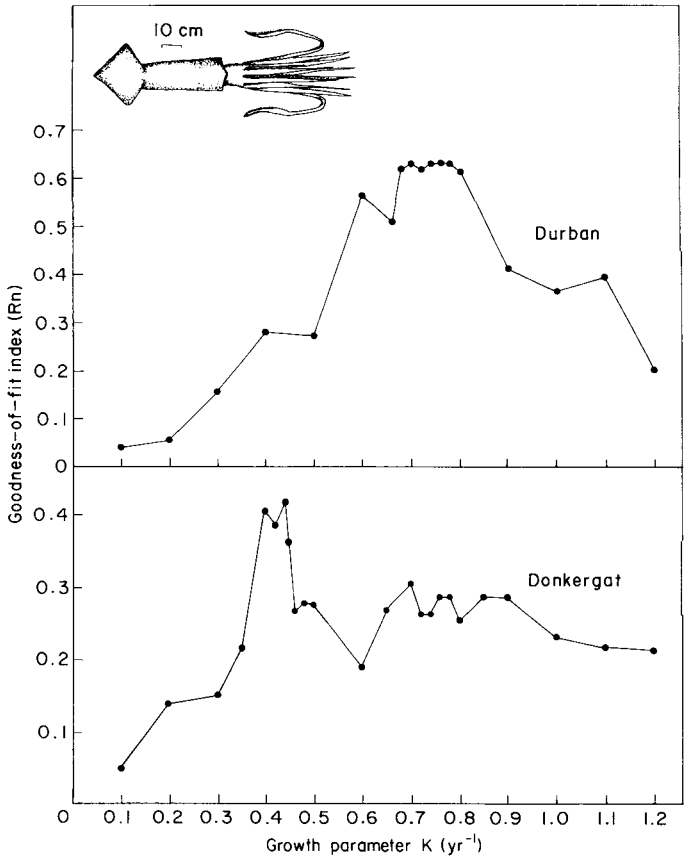

Figure 2. Plots of the goodness-of-fit index of the ELEFAN I program ($R_n = 10^{ESP/ASP}/10$) vs. input values of K, from $L_\infty = 2$, $C = 0.4$, and $WP = 0.7$.

was computed for different values of K. This last parameter is crucial, as it determines how fast L_∞ is approached and hence also correlates, in fishes with natural mortality and longevity (Pauly, 1980).

The maximum reported lower beak length of 2.1 cm, corresponding to a mantle length of 87 cm (Clarke, 1980), was used as estimate of asymptotic length. Conversion of length to weight was performed using:

$$\log_{10} W = 2.78 + 5.24 \log_{10} LRL \quad (2)$$

where W is the body wet weight (in g), and LRL the rostral length of the lower beak (in cm) (Clarke, 1980).

The postulated value of $C = 0.4$ was estimated from the empirical relationship between C in fishes and aquatic invertebrates and the summer-winter temperature difference of their habitat (Longhurst and Pauly, 1987). Finally, the external estimate of WP was set at 0.7 year, the coldest period in (southern) winter.

In addition to the lower beak length frequencies, a von Bertalanffy growth curve (without seasonality), i.e.

$$L_t = L_\infty(1 - \exp(-K^*(t - t_0))) \quad (3)$$

was fitted to growth data obtained by Clarke (1965,[1] 1980, and see Table 2) from the distance between cyclic growth structures on the beaks (similar to those on fish otoliths; for details on measurement see Clarke, 1965).

Comparisons of growth performance

For purely statistical reasons, different estimates of asymptotic size for equations such as (1) or (3) will tend, to some extent, to be inversely correlated with the corresponding estimates of the parameter K. However, more than just a statistical artefact is involved; organisms with high asymptotic sizes tend to have low values of K, whatever the fitting method. When corresponding pairs of L_∞ and K values, or better of W_∞ (the weight corresponding to L_∞) and K values, are plotted on double logarithmic paper, this results in the growth parameters of related organisms forming ellipsoid scatterplots which show low variability

[1]The specimens used by Clarke (1965) were later reidentified as *Kondakovia longimana* (Clarke, 1980).

Table 3. Growth parameters of squids, as used to infer their position on an auximetric grid (see also Fig. 3).

Species	Area	L_∞ (cm)	W_∞ (g)	K (yr^{-1})	Source
1 *Todarodes pacificus* (fem.)	Northwest Pacific	28.1	461	0.24	Okutani (1983)
2 *Todarodes pacificus* (male)	Northwest Pacific	25.8	349	0.28	Okutani (1983)
3 *Loligo gahi*	Southern Chile	37.0	410	0.34	Arancibia and Robotham (1984)
4 *Loligo opalescens*	California	20.8	125	0.76	Fig. 1, based on Spratt (1978) and Fields (1965)
5 *Loligo pealei*	Gulf of Mexico	23.0	207	0.95	Pauly (1965), partly based on Lange and Johnson (1981)
6 *Loligo pealei*	Off New Zealand	38.3	680	0.59	Pauly (1965), based on Ikeda and Nagasaki (MS, 1975), and Lange and Johnson (1981)
7 *Loligo chinensis*	Gulf of Thailand	40.9	704	0.49	Supongpan (1988)
8 *Loligo duvauceli*	Gulf of Thailand	26.6	265	0.84	Supongpan (1988)
9 *Sepioteuthis lessoniana*	Southern India	27.0	650	0.73	Longhurst and Pauly (1987)
10 *Onychoteuthis boreali japonica*	East of Hokkaido	40.0	1575	0.47	Pauly (1985), based on Okutani and Murata (1983)
11 *O. boreali japonica* (male)	East of Hokkaido	35.0	1600	0.48	Pauly (1985), based on Okutani and Murata (1983)
12 *Illex illecebrosus* (fem.)	Off Eastern Canada	29.4	500	0.65	Pauly (1985), based on Lange and Sissenwine (1983)
13 *Illex illecebrosus* (male)	Off Eastern Canada	23.9	290	1.08	Pauly (1985), based on Lange and Sissenwine (1983)
14 *Illex illecebrosus*	Northwest Atlantic	32.0	600	2.50	Pauly (1985), based on Au (MS, 1975) and Lange and Johnson (1981)
15 *Loligo duvauceli* (fem.)	Southern India	23.8	276	1.70	Meiyappan and Srinath (1989)
16 *Loligo duvauceli* (male)	Southern India	37.2	590	1.10	Meiyappan and Srinath (1989)
17 *Dosidicus gigas*	Gulf of California	96.0	22 000	1.20	Pauly (1985), based on Erhardt *et al.* (1983)
18 *Kondakovia longimana*	Antarctica	85.2	29 400	0.44 (?)	This paper, based on Clarke (1980); See text.

and define the growth performance of the taxon to which the organisms belong (Pauly, 1979; Longhurst and Pauly, 1987).

Results

Figure 2 shows plots of the goodness-of-fit index Rn vs. K for *K. longimana* with the parameters $L_\infty = 2.1$ cm, $C = 0.4$, and WP = 0.7 year. Figure 2a shows that, for the data collected at Durban, a maximum of Rn was obtained with $K = 0.8\ yr^{-1}$. For the data collected at Donkergat (Fig. 2B), a maximum was obtained at $K = 0.4\ yr^{-1}$. Combining the two data sets led to similar results, i.e. it was not possible to determine unambiguously the growth coefficient K from these data.

The von Bertalanffy curve fitted to the beak growth structures data of Table 2 yielded an extremely good fit. As the relation between growth bands and absolute age is unknown, time increments of 3, 4, and 6 months were considered as growth period between the bands, resulting in estimates of $K = 0.8\ yr^{-1}$, $0.6\ yr^{-1}$, and $0.4\ yr^{-1}$, respectively, and covering the above range of K values. The estimated asymptotic beak length was 2.34 cm in all three cases, corresponding to an asymptotic dorsal mantle length of 98 cm.

Table 3 presents our compilation of growth parameters for squids, most of which derive from analysis of modal progression in length frequencies and for which the problem of aging does not therefore arise. Figure 3 presents the auximetric grid that forms, along with the above results, the basis of our discussion.

Discussion

Figure 3 suggests that squids generally have a growth performance similar to that of the slower-growing species among the scombrids. There is also some indication that some groups (e.g. *Todarodes*, see nos. 1 and 2 in Fig. 3) may have a lower growth performance, comparable to that of clupeids.

Some extremely high growth performances, such as reported for *Illex illecebrosus* by Amaratunga (1980), may

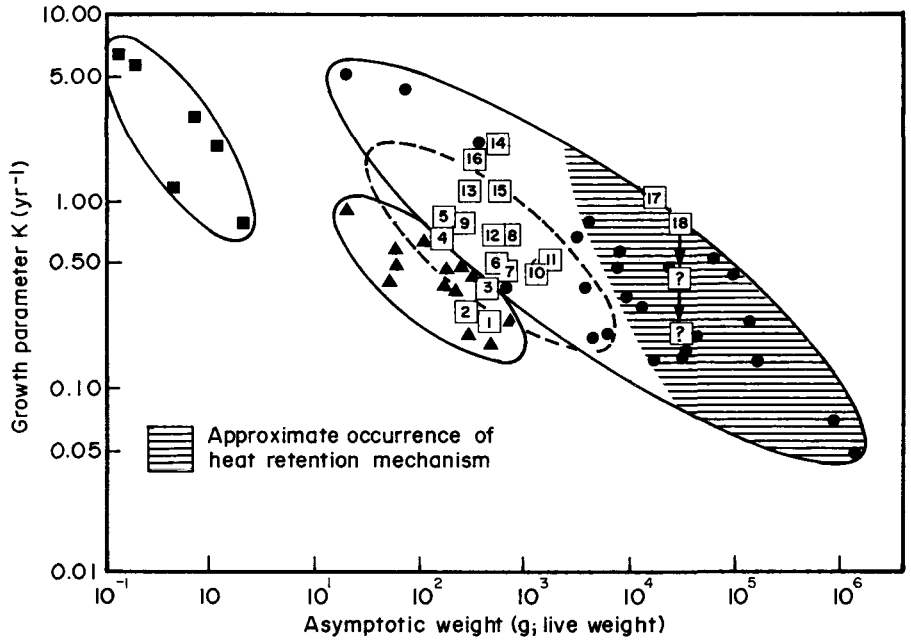

Figure 3. Auximetric grid showing ellipsoids for Cyprinidontidae (= guppies), Clupeidae (herring and sardine), Scombridae (mackerel and tunas) and various squids (from Table 3). The shading indicates the area where metabolic rate is so high that the scombrid species in question maintain a temperature higher than that of the environment (shaded area adapted from Table 1 in Carey *et al.*, 1971). ■ = Cyprinidontidae, ▲ = Clupeidae, ● = Scombridae, □ = Various squids.

probably be incorrect, given that other well-documented estimates exist for the same species which match those of other squid species of the same size range (see Table 3 and Fig. 3, nos. 12, 13, 14). The information given by Lee *et al.* (1989) for *Sepioteuthis lessionana* raised in captivity does not allow for estimation of growth parameters, hence this species could not be included in our comparisons.

The extremely high growth rate reported by Erhardt *et al.* (1983) for *Dosidicus gigas* (no. 17 in Table 3 and Fig. 3) may also be questionable: it implies a metabolic rate far in excess of that reported from the most advanced scombrids. The high metabolic rate of these scombrids has led to numerous anatomical adaptations, especially the complex counter-current systems that have evolved to retain such heat (see Carey *et al.*, 1971 and contributions in Sharp and Dizon, 1978). To date, such adaptations have not been reported from even the most active and largest squids, which argues against their having a metabolic rate as high as or even higher than those of large scombrids.

This brings us back to *K. longimana*. The above bioenergetic considerations suggest that the growth parameters estimated from a curve between "C and D" in Figure 75 of Clarke (1980), i.e. with a three months' interval between the growth bands and, correspondingly, with $K \geq 0.8\ yr^{-1}$ (on or above square 18 in Fig. 3), are too high. Such fast growth would also not be supported by the plots in Figure 2a or 2b. In Figure 3 the square directly below square no. 18 shows the position which *Kondakovia longimana* would take on the auximetric grid if the peak at $K = 0.4\ yr^{-1}$ in Figure 2b was accepted. We believe that this K value is still too high, but cannot demonstrate this because the data of Table 1 lack the small, fast-growing animals from which reliable estimates of K could be obtained and hence growth rate safely inferred. Accepting $K = 0.4\ yr^{-1}$, which implies that the growth structures in Table 2 would be 0.5 year apart, implies in any case a longevity of at least 4–5 years, which is 2–3 times that assumed earlier.

Ecological reasoning, taking into consideration the strong annual pulse in Antarctic waters, might even indicate a 12 months' period for those growth bands, further reducing K (to $0.2\ yr^{-1}$, Fig. 3) and increasing longevity to 8–10 years, as also briefly discussed by Clarke (1965). These considerations strongly suggest the need for new studies on the growth of large cephalopods, through which their true age and related vital statistics (e.g. mortality, production/biomass ratio, etc.) could be established.

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